

The Mating System of Three Territorial Butterflies in Costa Rica

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Abstract. Territorial behavior was observed in three Costa Rican butterfly species whose males perch in sunspots and open areas along a forest stream. Males of *Calaenorrhinus approximatus* occupied sunspot clearings for 1-2 hr in the early morning, with the same individual defending a site for up to 19 days. Males of *Astraptes galesus cassius* perched on the broad leaves of a piper in a tree fall clearing by the stream, with one individual returning for 17 days as the territory holder. Males of *Mesosemia asa asa* perched in streamside vegetation with a maximum territorial tenure of 25 days. Territorial males of all three species regularly patrolled the area about their perching sites and responded to intruders with circling chases and ascending pursuit flights. One mating occurred in the territory of a *C. approximatus* male, and three were recorded for *M. asa* in or near a perch territory. The mating systems of these species appear convergent with other butterflies whose males defend landmark territories.

Introduction

Although there is a growing literature on butterfly mating systems (reviews by Ehrlich, 1984; Rutowski, 1982, 1984), little is known about the mating tactics of tropical butterflies. Here I describe the territorial and mate-locating behavior of two skippers (*Celaenorrhinus approximatus* Williams & Bell and *Astraptes galesus cassius* Evans) and a riodinid butterfly (*Mesosemia asa asa* Hewitson), demonstrating that these butterflies have convergently evolved a number of similarities in their mating systems. I then compare their behavior with that of a number of temperate-zone species with similar tactics.

Materials and Methods

Calaenorrhinus approximatus Williams & Bell

On the basis of two specimens, one taken outside the study period, the skippers I studied were assigned to *Celaenorrhinus approximatus*, although another very similar species, *C. eligius*, also occurs in Costa Rica (John Burrn, pers. comm.). This skipper was observed at two locations separated by about 2 km along the Rio Guacimal, a 2-3 m wide and 0.5 m deep stream that flows through lower montane wet forest at 1300 m in Monteverde, Costa Rica. The study took place from 26 April to 14 July 1986 with the observer capturing and

marking six males with Liquid Paper Typing Correction Fluid while relying on natural wing tears to identify five other individuals. I observed sites occupied by males beginning about 0800-0900. I recorded the identity of the male or males at the location over a period of several hours, while also on some days noting the number of male-male aggressive interactions, their duration, the number of patrol flights made by the male perching in the area, and the time spent in each flight.

Astrartes galesus cassius Evans

The study of this skipper took place in one of the two locations where *C. approximatus* was observed. Nine males were captured and marked with Liquid Paper during the period from 7 June to 30 July 1986. On all but 5 days I checked the perching area at intervals during the morning to record the identity of the male or males present. On some days the butterflies were observed continuously for 15 min to 1 hr in order to record the frequency of social interactions, and the duration of flights taken by the male perching at the site.

Mesosemia asa asa Hewitson

I watched this riodinid butterfly at two stream sites separated by about 150 m. I captured and marked (with Liquid Paper) eight males; five other males were identified through their distinctive patterns of wing damage. The sites were monitored from 7 June to 30 July 1986 to record which males perched there. Some days one or more males was selected for continuous observation for 15 min to 1 hr, during which time social interactions, patrol flights, and their duration were noted.

The data collected provide a picture of the daily activity pattern and the nature of territoriality of males of the three species. In addition, for two of the species, *C. approximatus* and *M. asa*, incidental observations of male-female interactions permit a description of mating behavior.

Means are presented ± 1 S.D.

Results

Daily Activity Pattern of *Celaenorrhinus approximatus*

On sunny days males flew to and perched upon leaves within sunspots 2-4 m in diameter that were located within 10 m of the Rio Guacimal. At one sunspot selected for special study between 1-14 May 1986, the first male appeared between 0801-0906 ($\bar{X}=0834$, $N=10$ days). At a second sunspot 2 km upstream the first male arrived between 0836-0910 ($N=4$ days). On overcast mornings, arrival times could be delayed until 1100.

Once have perched, usually on a broad-leaved plant less than 0.5 m from the ground, the male engaged in frequent patrol flights in which he darted about the sunspot. At both sites, resident males not only patrolled the sunspot at which they had arrived, but also occasionally visited and perched in one to three other sunspots up to 30 m distant. These patrol flights lasted from 3-32 sec ($\bar{X}=10.4 \pm 5.7$ sec; $N=60$ flights

by 5 males). The frequency of these flights was 1.01/min based on a total of 80 min of observations of three males on four days.

Typically males ceased flying about sunspots at some time between 0930-1030 on sunny days with the male alighting upside down under a leaf after a flight about the sunspot. Flight activity averaged 76.3 ± 18.5 min ($N=7$ days).

Site Tenacity and Territoriality

I identified six individuals at the same sunspots on 4 to 10 dates with a mean interval between first and last sighting of 12 ± 3.5 days. Some of the returning skippers stayed only briefly on any given day but others occupied the site for most or all of the morning activity period. These individuals, referred to hereafter as resident males, dashed after any conspecifics that flew near them. The two males would then chase one another in tight circles about the sunspot. Circle chases always preceded ascending flights, in which the two combatants flew up and away from the sunspot in near vertical flight into the forest canopy. Some interactions consisted of a series of circle and ascending flights, with the two rivals descending separately after an ascent and returning to the sunspot to repeat the cycle anew.

The frequency of aerial fights was 9.5/hr ($N=10.9$ hrs of observation). The mean duration of these contests was 46.4 ± 42.0 sec ($N=34$ fights recorded on 11 days). Intraspecific chases lasted much longer on average than either patrol flights ($\bar{X}=10.4$ sec, see above), or flights triggered by other passing butterflies, tachinid flies and damselflies ($\bar{X}=4.7 \pm 2.1$ sec, $N=24$ chases recorded on 4 days).

In 66 of 85 fights, only one male returned to perch in the sunspot after a circle flight or ascending flight. In 63 of 66 cases, the sole returning male was the resident male who had occupied the site first that day. When two males did land in the same sunspot after an aerial chase, it was generally only a matter of a minute or two before one male patrolled the sunspot eliciting a new chase and (usually) the departure of the newcomer.

Ousters of territory-defending males were observed three times. On 1 May an unmarked male with fresh undamaged wings displaced *yellow* after a long series of aerial chases. Twice males that had been residents on preceding days arrived late at their sunspot to find the site occupied by another male; in both cases turnovers occurred, with the previous day's resident quickly ejecting the newcomer.

Thus the general pattern was for one male of claim a perch site for all of the morning activity period over several days. Other males, including previous residents, might visit the site over a number of days but they did not remain long.

Male-Female Interactions

I saw one copulation in about 20 hr of observation. This mating was discovered after its inception when I noticed that the resident male was

no longer perching in his sunspot. In his place was an unmarked individual. The resident was under a broad leaf within his territory copulating with an apparently fresh female with unworn wings. If the mating occurred at about the time when the resident disappeared from view, the duration of copulation would be about 1 hr.

Daily Activity Pattern of *Astraptes galesus cassius*

Males of *A. g. cassius* came in the morning to a stand of broad-leaved *Piper auritum* (Piperaceae) growing at the edge of the Rio Guacimal. On six sunny mornings between 7 June and 13 July, the first male to perch on an exposed piper leaf appeared before 0830 (0808 was the earliest record). On cloudy days arrivals were delayed, but one or more males perched on the piper for at least brief periods on 30 of 36 days during the study, even if the sun did not shine. Activity ceased in steady rain but otherwise males remained at the site until some time between 1100-1200 (the latest record was 1157). Thus males were active 2-3 hr per day.

The leaves used as perches were 2-3 m above the ground with the primary perch site situated in the middle of a large (roughly 15 m diameter) clearing created by tree falls. The piper received direct sunlight only for a short period during the latter part of the morning. Perching males often flew out from and returned in a few seconds to the same leaf. Longer (10-20 m) patrol flights along the stream course lasted from 4 to 25 sec with a mean of 10.2 ± 4.2 sec ($N = 79$ flights of 5 males on 7 days). The frequency of patrol flights was 39.3/hr (4.5 hr of observations of 4 different males on 8 dates).

Site Tenacity and Territoriality

Marked individuals often returned to the piper patch over many days and stayed for several hours each morning (Table 1). The resident male chased intruders in straight horizontal pursuits and ascending flights that were not as structured as the circle/ascending flights of *C. approximatus*. Visitors usually left the area quickly when pursued. Male-male interactions occurred an average of 16.6 per hr ($N = 5.5$ hr observation of 4 residents). Chases of conspecifics lasted an average of 25.3 ± 12.6 sec ($N = 39$).

A change in territory ownership occurred on 7 occasions (Table 1) during 52 days. The new males all had less damaged wings than the old residents that they replaced after a number of chases. Previous residents continued to return to the site on subsequent days in 4 cases (Table 1), often coming earlier than their replacements. For example, on 24 June, *green* occupied the central piper plant from 0919-0952, giving way only when *yellow* finally arrived (*yellow* having claimed the territory on 16 June). Although past residents were always quickly displaced by the new owner, at least one male (*yellow*) succeeded in reclaiming the site

Table 1. Identified males of *Astraptus galesus cassius* at one site from 7 June to 28 July 1986. R=resident territory owner, v=non-territorial visitor, R*=males loses territory to rival.

Male	June	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23		
pink		R---R*				v					v						v			
green		R	-----	-----	-----	-----	-----	-----	-----	-----	R*	v	v	v	v					
yellow o/o											R	-----	-----	-----	-----	-----	-----	-----	-----	
	June	24	25	26	27	28	29	30	July	1	2	3	4	5	6	7	8	9	10	11
pink			v																	
green		R*	v		v	v		v				v	v	v						
yellow o/o		R---R*		v	v			R	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
blue		R	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	July	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28		
pink																				
green																				
yellow o/o		R*	v																	
blue																				
wing mark		R	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
yellow ii								R	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	R*
wing notch																				R

for 12 more days (Table 1) when the male that had defeated him failed to reappear on 30 June.

Daily Activity Period of *Mesosemia asa asa*

Males arrived at their streamside perches between 0930-1030 (N=12 days) and they departed on sunny afternoons between 1400-1500 (N=3 days) with one record of a male present until 1516. The butterflies perched on exposed leaves 0.5 to 1.5 m above the ground, and they faced out into the open space created by the stream channel. Early in the morning males often selected sites that were in full sun, but they were active even when all perches were shaded.

During 6 hr of watching five males, I recorded 14.3 perch shifting flights of 1-3 sec per hr. Longer patrol flights of 3 m or more lasting on average 9.1 ± 4.6 sec (N=14) occurred at the rate of just 3.8 per hr during this same period.

Territorial Behavior

Along a 150 m stretch of stream there were only four perching sites,

on the underside of a leaf with the male alighting beside her. Copulation followed quickly with minimal courtship; " T_f " (Burns, 1970) was exactly 52 min in one case, while copulation lasted between 40-75 min in the two other cases.

Discussion

Table 3 provides a summary of male behavior in the three butterflies. There are both differences and similarities in the mating system of these unrelated species. The butterflies differ in the timing and duration of their daily mate-locating activity, but each species is active for only a fraction of each day. All three species perch in relatively open areas, with *Celaenorrhinus* especially dependent on sunspots. These areas are not only relatively free from visual obstruction so that males may detect passing females, but may also offer thermoregulatory advantages in cool rainforest habitats. Males of the two skippers patrol their territories often, whereas the riodinid *M. asa* flies from perches infrequently. Territorial males of all three species engage intruders in ascending flights (although speed of flight varies greatly among species). Residents are able to control their perching areas up to two weeks or more, but they encounter receptive females at very low frequency.

Callaghan (1982(83)) has documented similar behavior in a number of other tropical riodinids whose males wait on perches along the very edge of forests or in treefall areas; Scott (1974, 1975, 1982) has observed some North American skippers in which male mate-locating activity is concentrated in gulches and ravine bottoms. In these cases, males appear to take advantage of natural features that channel females past certain points. Similarly, hilltopping species (Shields, 1967; Scott, 1970), seem to be making use of conspicuous topographic features that may guide the movements of females. Landmark-based mating systems

Table 3. A comparison of the mating system of two territorial stream-side skippers, *Celaenorrhinus approximatus* and *Astraptes galesus*, and the riodinid butterfly, *Mesosemia asa*.

	<i>C. approximatus</i>	<i>A. galesus</i>	<i>M. asa</i>
Activity period	< 2 hr 0830-1030	ca. 3 hr 0830-1130	ca. 4 hr 1000-1400
Patrol flights - frequency: mean duration	60/hr: 10 sec	39/hr: 10 sec	3.8/hr: 9 sec
Fights-frequency: mean duration	9.5/hr: 46 sec	16.6/hr: 25 sec	5.5/hr: 25 sec
Observed matings	1	0	3
Maximum territorial tenure	19 days	21 days	25 days

apparently evolve when males cannot profitably search for mates at larval foodplants or adult nectar sources (Thornhill and Alcock, 1983).

Territoriality is widespread in the landmark and sunspot mating system group (e.g. Shields, 1976; Davies, 1978; Bitzer & Shaw, 1979(80); Callaghan, 1982(83); Lederhouse, 1982; Wickman & Wicklund, 1983; Alcock, 1983, 1985; Alcock & O'Neill, 1986). Males typically compete for landmark territories with elaborate circling and vertical ascending flights (see also MacNeill, 1964). These interactions appear to involve demonstrations of speed and aerial agility to rivals, as well as endurance in those cases in which repeated vertical pursuit flights occur.

Convergent evolution is also evident in the behavior of females of this group, which fly toward perched males, leading them on a slower, more direct pursuit flight than that seen in male-male fights. Females that are receptive alight quickly, and males land beside them to offer only the briefest of courtships before copulation occurs (e.g. Alcock, 1985; Alcock & Gwynne, in press; Wickman & Wiklund, 1983).

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Literature Cited

- ALCOCK, J., 1983. Hilltopping territoriality by males of the great purple hair-streak, *Atlides halesus* (Lepidoptera: Lycaenidae): Convergent evolution with a pompilid wasp. *Behav. Ecol. Sociobiol.* 13: 57-62.
- , 1985. Hilltopping in the nymphalid butterfly *Chlosyne californica* (Lepidoptera). *Amer. Midl. Nat.* 113: 69-75.
- ALCOCK, J. & D.T. GWYNNE, In press. The mating system of *Vanessa kershawi*: Males defend landmark territories as mate encounter sites. *J. Res. Lepid.*
- ALCOCK, J. & K. O'NEILL, 1986. Density-dependent mating tactics in the Grey hairstreak, *Strymon melinus* (Lepidoptera: Lycaenidae). *J. Zool.* 209: 105-113.
- BITZER, R.J. & K.C. SHAW, 1979(80). Territorial behavior of the red admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae). *J. Res. Lepid.* 18: 36-49.
- BROWER, L.P., J.V.Z. BROWER, & F.P. CRANSTON, 1965. Courtship behavior of the queen butterfly, *Danaus gilippus berenice* (Cramer). *Zoologica* 50: 1-39.
- BURNS, J.M., 1970. Duration of copulation in *Poanes hobomok* (Lepidoptera: Hesperiiidae) and some broader speculations. *Psyche* 77: 127-130.
- CALLAGHAN, C.J., 1982(83). A study of isolating mechanisms among neotropical butterflies of the subfamily Riodininae. *J. Res. Lepid.* 21: 159-176.
- DAVIES, N.B., 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): The resident always wins. *Anim. Behav.* 26: 138-147.
- EHRlich, P.R., 1984. The structure and dynamics of butterfly populations. *Symp. R. Ent. Soc. Lond.* 11:25-40.

- LEDERHOUSE, R.C., 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. Behav. Ecol. Sociobiol. 10: 109-118.
- MACNEILL, C.D., 1964. The skippers of the genus *Hesperia* in western North America with special reference to California (Lepidoptera: Hesperidae). Univ. Calif. Publ. Entomol. 35:1-230.
- RUTOWSKI, R.L., 1982. Mate choice and lepidopteran mating behavior. Fla. Ent. 65: 72-82.
- , 1984. Sexual selection and the evolution of butterfly mating behavior. J. Res. Lepid. 23: 125-142.
- SCOTT, J.A., 1970. Hilltopping as a mating mechanism to aid the survival of low density species. J. Res. Lepid. 7: 191-204.
- , 1974. Mate-locating behavior of butterflies. Amer. Midl. Nat. 91: 103-117.
- , 1975. Mate-locating behavior of North American butterflies. J. Res. Lepid. 14: 1-10.
- , 1982(83). Mate-locating behavior of western North American butterflies. II. New observations and morphological adaptations. J. Res. Lepid. 21: 177-187.
- SHIELDS, O., 1967. Hilltopping. J. Res. Lepid. 6: 69-178.
- THORNHILL, R. & J. ALCOCK, 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Mass. 547 pp.
- WICKMAN, P.-O. & C. WIKLUND, 1983. Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). Anim. Behav. 31: 1206-1216.